

## Adaptive Strategies of Feeding and Predator-Avoidance in the Larvae of the Neotropical Butterfly, *Morpho peleides limpida* (Lepidoptera: Morphidae)

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**Abstract:** The daily pattern of movement and feeding was studied for ten successive days in the larvae of the tropical butterfly, *Morpho peleides limpida* Butler, at a locality in central Costa Rica where this insect is unusually abundant. The major findings of these studies are: (1) larvae during all five instars are dawn-dusk feeders, with the average feeding time ranging between 20–35 minutes at each peak of activity, (2) movement is associated solely with commencement and termination of feeding since larvae have stable resting positions removed from feeding sites, and (3) the bimodal feeding activity is apparently under control of changes in light intensity. The adaptive significance of this larval feeding behavior is discussed in terms of the broad host plant specificity and apparent automimicry in this butterfly, and is interpreted as a mechanism for reducing predatory attack by visual vertebrate predators. Finally, it is hypothesized that only those species of *Morpho* which have experienced selective pressures molding them into successful second-growth forms evolve such feeding behavior, presumably as an additive measure for reducing predation from generalized visual vertebrate predators while exploiting a broad range of larval host plants. More highly specialized species of *Morpho* associated with primary-growth lowland tropical wet forests are predicted to lack such a behavioral pattern since (1) their larvae feed on fewer plant species, (2) the few local larval host plants are high in toxic secondary compounds, and (3) visual vertebrate predators in more stable tropical communities are themselves more specialized feeders and thus fewer species would consistently exploit *Morpho* larvae as a food source.

### INTRODUCTION

This paper is one in a series concerning the evolutionary biology of New World neotropical butterflies belonging to the genus *Morpho* (Lepidoptera:

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Morphinae). Previous reports (Young, 1971a, b, c) have dealt primarily with adult ecology and behavior in selected species of *Morpho*, but this present paper describes a daily pattern of moving and feeding behavior in the larvae of a "brownish morpho" (Young, 1971b), *Morpho peleides limpida* Butler. This butterfly, which ranges from Venezuela to Mexico (Seitz, 1924; Le Moult and Real, 1962), is extremely widespread throughout the montane and lowland wet forests of Central America, occurring as at least 15 varieties. Zoogeographical studies (Seitz, 1924; Le Moult and Real, 1962; Blandin and Descimon, 1970) emphasize that *Morpho peleides* represents the major extension of the South American *achilles* group into Central America. A major aspect of this expansion has involved a long evolutionary history in members of the *achilles* group for adaptation to inhabiting less stable second-growth plant communities whereas most other species-groups of *Morpho* have remained associated with lowland primary-growth tropical wet forests. Therefore, taxonomic, behavioral, and ecological studies of *Morpho peleides* at different parts of its extensive geographical range should prove of interest in elucidating the widespread geographical expansion of the butterfly.

The studies herein reported concern *peleides limpida* at a montane wet forest site in central Costa Rica. The major findings of these descriptive studies are: (1) larvae of all instars exhibit a marked bimodal joint locomotor and feeding activity pattern over a 24-hour period, with peaks occurring at dawn and dusk; (2) younger larvae (instars 1-2) consistently begin to move and feed earlier in the evening and later in the morning than do older larvae (instars 3-5) on the same host plants. This displacement in daily activity pattern associated with instar is herein hypothesized to be a result of a change in resting position of larvae as they grow larger, causing temporal shifts in the registering of critical light intensities believed to initiate peak activity periods. The adaptive significance of such behavior in the larvae of *Morpho peleides* is also discussed in terms of an hypothesis which accounts for observed local broad host plant specificity, a defense strategy involving automimicry, and the local palatability spectrum for larvae. The adaptive significance of dawn-dusk feeding as related to marked differences in habitat selection exhibited by different species-groups is also discussed.

#### METHODS

In conjunction with studies of the life history and seasonal population structure of *Morpho peleides limpida* (Young and Muysshondt, 1972a), were observed on several different host plants at one locality in central Costa Rica. Observations on the feeding activity and related behavior of larvae were made at Cuesta Angel de Sarapiquí, a montane tropical wet forest (Holdridge, 1967) region of about 1000 meters elevation in the Alajuela Province. Observations were restricted to a narrow strip of early second-growth vegetation situated on



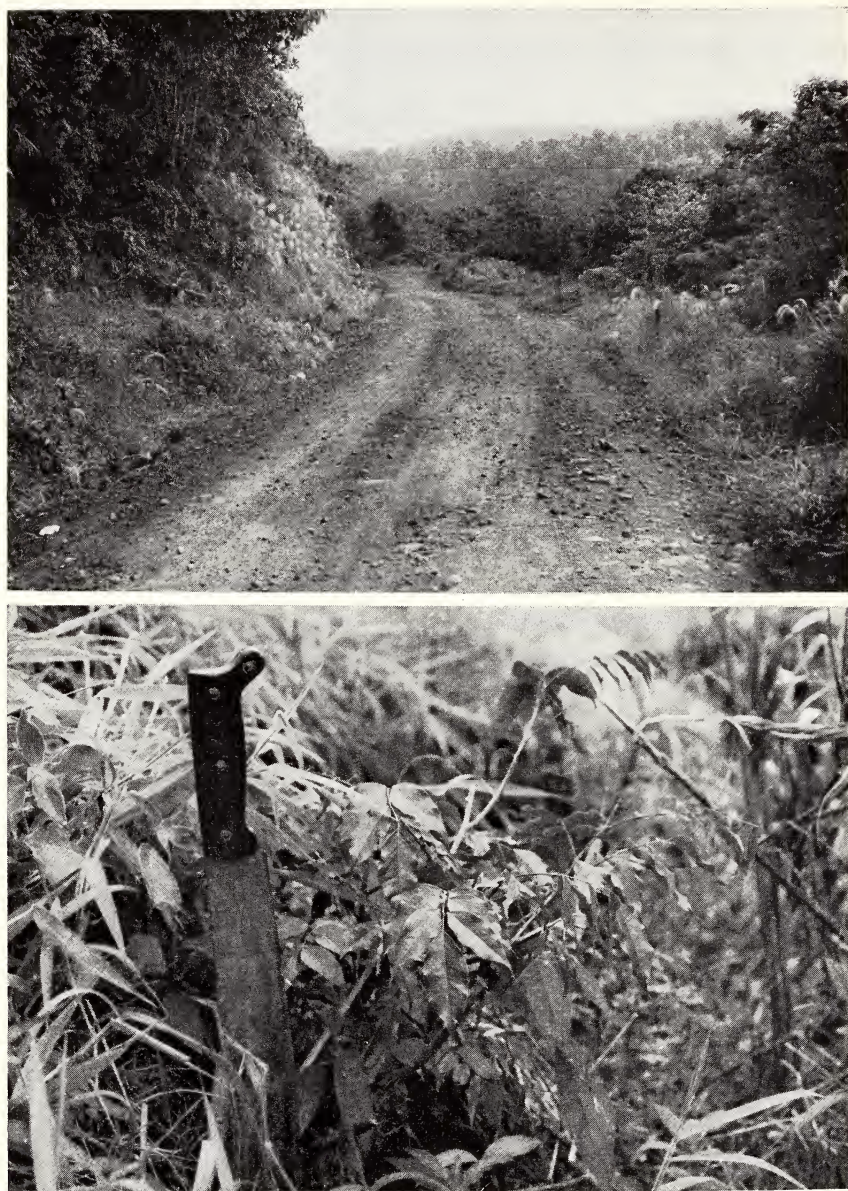


FIG. 1. Above: the second-growth habitat at Cuesta Angel, Heredia Province, Costa Rica (about 1000 m. elev.) where larval behavior in *Morpho peleides* was studied during June–September, 1971. Larvae were abundant on small seedlings of *Machaerium seemannii* (Leguminosae) growing under a cover of tall grass on the steep slope directly to the left of the dirt road. Below: the typical seedling size of *Machaerium seemannii* in which eggs and larvae of *Morpho peleides* were most abundant. The tall grass has been cleared away to show the plant.

about a 25° slope and bordering a large coffee plantation on the west, and dropping off very steeply (about 60° incline) into virgin rain forest to the east. A one-lane dirt road (connecting San José with Puerto Viejo) ran along this strip of vegetation, (Fig. 1) giving access to this precarious study site situated about 5 miles south of Cariblanco de Sarapiquí. Due to the sloping terrain and soft earth, observations on larvae were made either by climbing these slopes, or by slowly working down sections of the slope on a rope harness.

A census of all life stages in a high density local population of *Morpho peleides* was started on June 25, 1971. The spatial distributions of eggs and larvae were examined in order to estimate rates of predation and parasitism. With associated data on the locations of larvae on different species of host plants, a study of diurnal feeding habits and other activities was begun on August 18, 1971. A series of ten successive days of observation on larval activity was obtained. On a day of observation, various instars were observed once every half-hour for 24 successive hours; data was recorded for individual larvae according to their instar, noting: position of the plant, resting periods, periods of movement, and periods of feeding. Movements of larvae between resting positions and feeding positions were also observed. By marking (with colored plastic tags) the individual host plants on which larvae were found, the same larvae were observed throughout the study period. Larval densities per individual host plant usually varied from one to four, often having first, second, and third instars together on a plant. This made it possible to determine the activities of different age-classes of larvae, on the same host plant, as well as on different individual host plants; this permitted variations in 24 hour activity patterns with respect to the microgeographic distribution of host plants (i.e., relative exposure of individual plants to shading effects of the undergrowth canopy). Unlike certain species of Brazilian *Morpho* (Seitz, 1924; Luis Otero, pers. comm.), the larvae of *Morpho peleides* are not gregarious and the movements of individual larvae on a plant are independent of one another.

Since females of *Morpho peleides* oviposit heavily on various host plants less than 2 meters tall observations of larval activity were restricted to plants less than this height. The most abundant larval host plant was *Machaerium seemannii* (Leguminosae), with larvae most frequently on plants less than one meter in height (Fig. 1). The low distribution of larvae facilitated their examination with minimal mechanical disturbance resulting from jarring host plants, especially considering the sloping nature of the terrain at the study site.

#### RESULTS

Despite high rates of parasitism on larval *Morpho peleides* the long developmental time (about 110 days) of this butterfly relative to the short study period (10 days) permitted study of activity patterns for a relatively unchanging number of larvae. Numbers of larvae relative to the abundance of



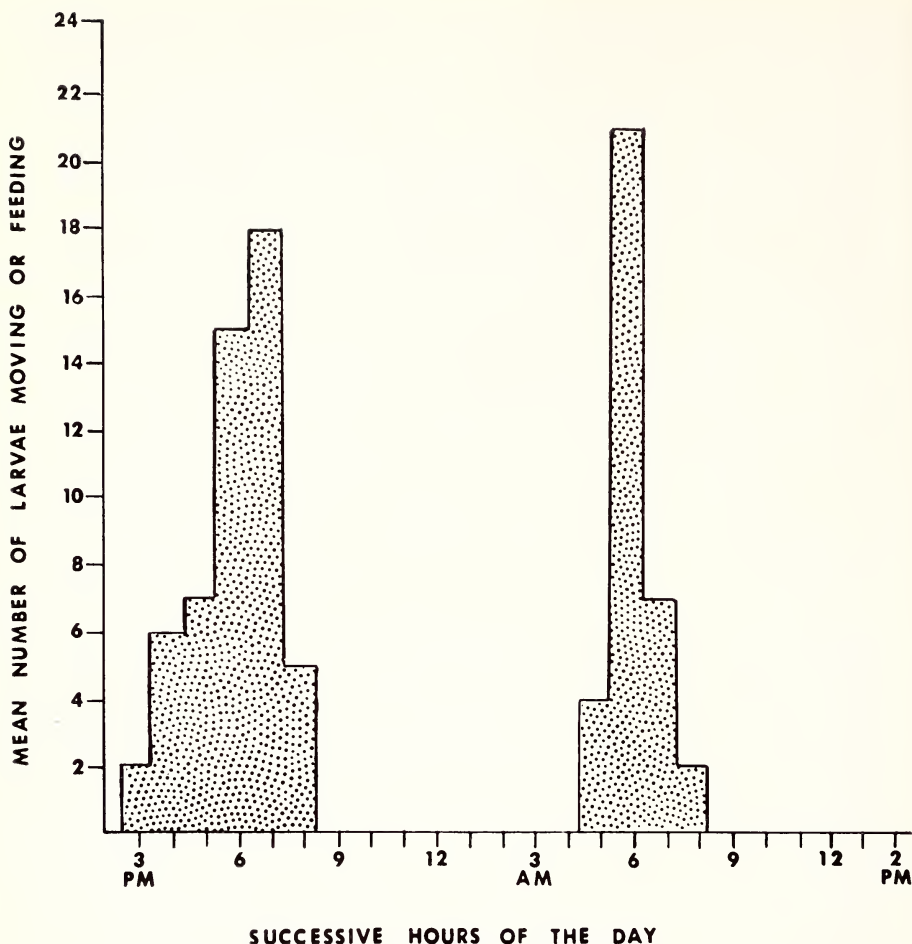


FIG. 2. The bimodal "dawn-dusk" daily pattern of movement and feeding exhibited by larvae of *Morpho peleides* at Cuesta Angel. Given are the mean numbers of larvae, all instars combined, seen at half-hour intervals, over a ten-day period. Measurements of activity patterns were made on the same larvae.

different host plants are summarized for the study period in Table 1. Of interest here is the fact that this butterfly undergoes successful development on several different host plants (listed in Table 1) in one locality. Since larvae were most abundant on *Machaerium seemannii* (Table 1), the bulk of observations on daily movement and feeding were limited to this plant species.

Larval feeding in *Morpho peleides* is markedly bimodal (Fig. 2), with peaks of feeding activity occurring during early morning and early evening hours. During the intervening hours of day and night, larvae are completely inactive

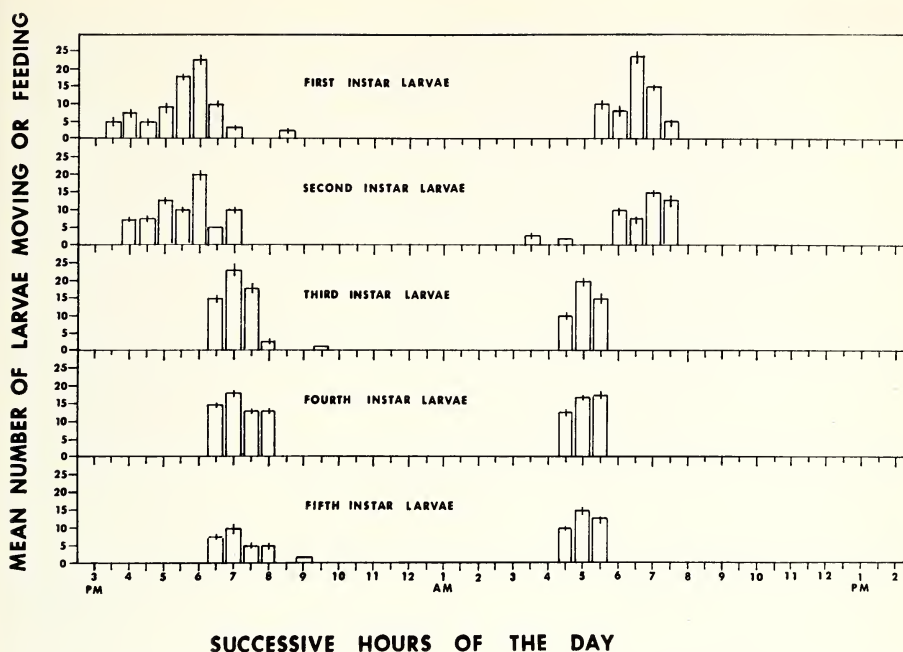


FIG. 3. Bimodal "dawn-dusk" daily pattern of movement and feeding in different instars of larval *Morpho peleides* at Cuesta Angel whose activity patterns are summarized in Fig. 1. The small vertical bars on each histogram unit are standard errors for the mean numbers of larvae moving and feeding during a given half-hour interval. There is a statistically significant shift (see text) in peak activity period occurring between second and third instar larvae.

and do not move at all. Movement appears to be associated exclusively with feeding activity and larvae crawl from resting positions to other sites for feeding. There is a marked temporal displacement in peak feeding periods at the beginning of the third instar of larval development (Fig. 3) resulting in third, fourth, and fifth instar larvae feeding later in the evening and earlier in the morning, relative to feeding peaks for first and second instars. A one-way analysis of variance for unequal sample sizes (Dixon and Massey, 1969) was employed to test the null hypothesis that there is no significant shift (temporal displacement) in feeding times among different instars. This hypothesis was rejected at  $P < 0.05$  ( $F$  value for "right side" of Fig. 3 is 9.62; for left side,  $F = 7.48$ ), with a significant shift in feeding times seen only between second and third instar larvae of *Morpho peleides*. The assumption of an infinite food supply necessary to use this test is justified since larvae do not experience crowding on individual host plants (Young and Muyschondt, 1972a). This pattern of temporal shift during ontogeny of *Morpho* is extremely consistent in



TABLE 1. Numbers of eggs and larvae of *Morpho peleides limpida*<sup>a</sup> on various host plants, from Cuesta Angel on the Caribbean slopes of Costa Rica.

| Host plant <sup>b</sup>           | Ranked <sup>c</sup><br>abundance | Eggs | Larval instar |    |    |    |   |
|-----------------------------------|----------------------------------|------|---------------|----|----|----|---|
|                                   |                                  |      | 1             | 2  | 3  | 4  | 5 |
| <i>Machaerium seemanii</i>        | 1                                | 82   | 51            | 43 | 20 | 19 | 9 |
| <i>Mucuna urens</i>               | 2                                | 52   | 33            | 21 | 15 | 10 | 4 |
| <i>Inga</i> sp-1                  | 3                                | 30   | 26            | 19 | 14 | 0  | 2 |
| <i>Machaerium donnell-smithii</i> | 4                                | 20   | 11            | 7  | 3  | 0  | 0 |
| <i>Pithecolobium</i> sp-1         | 5                                | 10   | 6             | 1  | 0  | 1  | 0 |
| <i>Inga</i> sp-2                  | 6                                | 6    | 4             | 0  | 2  | 0  | 0 |

<sup>a</sup> Given are the numbers of immature *Morpho* seen daily for ten successive days, August 22 through September 1, 1971. With few exceptions, numbers of immatures did not change during this period.

<sup>b</sup> Two other host plants, *Pterocarpus* sp-2 and *Lonchocarpus* sp-1, are not shown here since larval numbers were low.

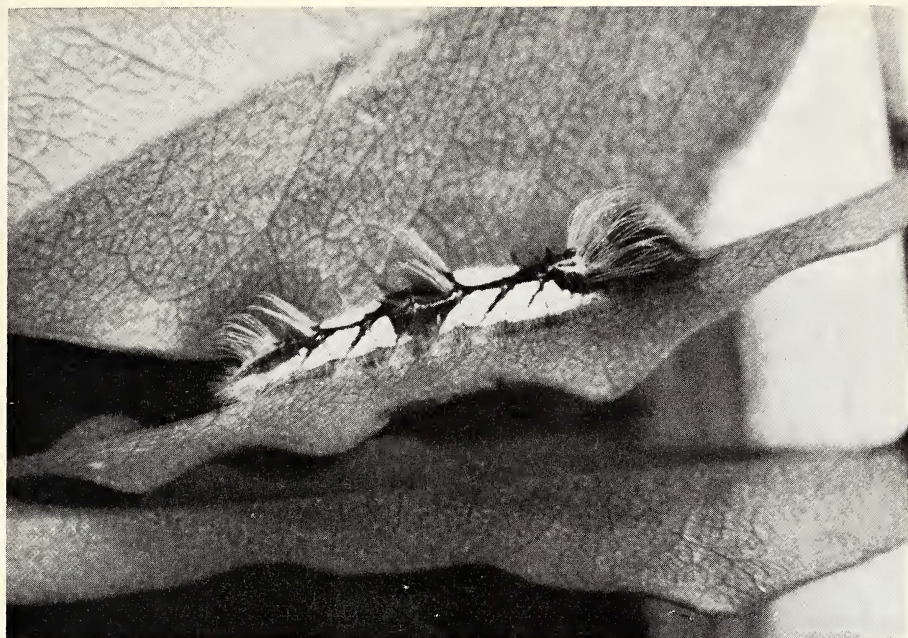
<sup>c</sup> In this ranking, 1 corresponds to the most abundant (population density) plant species exploited by *Morpho*.

field samples at Cuesta Angel, and has also been observed for larvae from a different locality, Bajo la Hondura, San Jose Province (also montane wet forest of about the same elevation as Cuesta Angel).

Regardless of instar, larvae of *Morpho peleides* separate their resting and feeding sites on *Machaerium*. This is essentially a vertical separation in later instars, while it is limited to adjacent leaves in younger instars. Younger larvae (first and second instars) always rest on the undersides of old leaves (Fig. 4) these being the leaves on which the eggs were deposited. Females lay their eggs singly, although as many as five eggs may be deposited on an individual plant by the same female on the same day. Eggs are laid on dorsal surfaces of older leaves (never on young leaves) and the first instar larvae, upon hatching, immediately crawl to undersides of these leaves. It is important to point out that females generally select leaves for egg deposition which are heavily shaded by the host plant—eggs are never laid on apical leaves exposed to direct sunlight. First instar larvae rest on the undersides of these well shaded leaves (Fig. 4), where they individually build small silken mats, and retain these resting sites through the second instar. Feeding takes place by movement to adjacent leaves, and seldom is the same leaf used as a resting site and a feeding site. Between late second instar and late third instar larvae acquire new resting positions on larger leaves near the exposed periphery of the host plant (Fig. 4).

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FIG. 4. Resting positions of the larvae of *Morpho peleides* on *Machaerium seemannii*. Right: early third instar larva resting on silken mat woven on the ventral surface of a leaf of the host plant. Larvae rest with head directed upward and the weight of the body causes the leaf to hang vertically. Until the middle of the third instar, larvae may rest on leaves, but become increasingly exposed to direct sunlight resulting from moving towards the periphery of the host plant (see text). Left: late fourth instar larva resting on a grass



stem at the base of the host plant. Larvae during the late third instar, and throughout the fourth and fifth instars become exposed to direct sunlight through the acquisition of resting positions not heavily-shaded by leaves of *Machaerium*.



By the time of the late third instar, larvae change their resting sites, now preferring to rest on even larger leaves near the ground, or else on branches of the host plant near the ground, or occasionally on branches of other plants in intimate contact with the host plant (Fig. 4). Barring any major disturbances, larvae retain these new resting sites until pupation. The dramatic lowering of resting sites on the host plant results in the development of a major and pronounced vertical movement associated with feeding. Third, fourth, and fifth instar larvae move from their individual resting sites near the ground to leafy regions in the uppermost one-third of the host plant, during feeding period (Fig. 3). As with younger larvae, older larvae individually construct thin silken mats for resting sites and always return to the same resting site upon termination of a feeding period. The changing of resting sites is apparently associated with increased size and weight of third instar larvae. They appear very awkward and remain only partially concealed on the smaller leaves associated with upper regions of the host plant, and owing to their extremely bright red and yellow patch work coloration, become noticeable targets for predator attack. The resting sites for all instars appear to function to conceal larvae when not feeding. The resting positions of larvae from the late third instar onwards are usually exposed to direct sunlight, despite the fact that fourth and fifth instars usually rest very close to the ground. This is attributed to the highly exposed plant growth form of *Machaerium* in which leaves do not form a small canopy over the seedlings. Furthermore, the seedlings are most abundant on exposed grassy slopes (Fig. 1). There is always a choice of a resting site (usually an older leaf or section of branch or stem—Fig. 4) that offers either a partial or completely unobstructed view of the sky, through the canopy of the undergrowth. Since individual larvae always return to the same resting sites after feeding, larvae during resting periods (Fig. 3) are always in direct contact with a general intensity of illumination which is not reduced from shadow effects of undergrowth. Relative to these older larvae, first and second-instar larvae, on the other hand, will register lower intensities of illumination *at any hour* during resting periods, since their resting sites are usually heavily shadowed by the undersides of *Machaerium* leaves. Such differences in resting site preference will in turn result in temporal shifts in the initiation of feeding activity (Fig. 3), assuming the latter to be under partial control of light intensity.

#### DISCUSSION

The data on the dawn-dusk locomotor and feeding activity pattern in larval *Morpho peleides* are discussed from three major standpoints: (1) A proposed mechanism for dawn-dusk feeding, (2) the adaptive significance of dawn-dusk feeding in larval *Morpho peleides*, and (3) dawn-dusk feeding as an adaptive strategy for the genus *Morpho*.



**A PROPOSED MECHANISM FOR DAWN-DUSK FEEDING:** The mechanism responsible for the bimodal feeding activity in larval *Morpho peleides* is undetermined, although it is suspected to involve an endogenous rhythm that can be modified by environmental factors such as heavy rainfall, strong winds, etc. Evidence suggesting such effects on the feeding rhythm comes from direct observation of larvae in the field under different environmental conditions: during heavy rainfall, larval feeding is postponed or halted. This also occurs during strong gusts of winds. Larvae that are feeding on individual host plants situated in heavily-shaded vegetation exhibit displaced feeding periods, *regardless of instar number*: in general, larvae in such shaded places begin feeding earlier (between 30–50 minutes) in the evening than larvae located on host plants in open, exposed places; the same larvae also begin to feed later in the morning (between 30 and 60 minutes later) than do larvae on exposed plants. However, no significant difference in larval numbers on shaded versus exposed plants was found—suggesting that oviposition occurs in both places in about equal frequency (assuming no differential rates of predation and parasitism between the two microhabitats). Again, this pattern resulting from microgeographic differences in larvae is consistent from day to day, and all instars exhibit such a difference in the commencement of feeding. These observations are interpreted as responses to changing intensity of illumination during the evening and dawn hours—larvae living on shaded plants register a lower intensity of illumination earlier than larvae on exposed plants in the same area. Larvae on exposed plants begin to feed earlier than those on shaded plants and the reverse pattern occurs for the dusk feeding period. Therefore, it appears that initiation of the two feeding periods is a response to changes in light intensity associated with the transition between day and night and vice-versa. It is less likely a response to temperature change since this would probably be less varying among different microhabitats than would light intensity resulting from the varied natures of vegetation cover in early second-growth habitats. However, temperature cannot be ruled out as a factor contributing to the regulation of bimodal feeding of larval *Morpho peleides* at this time; experiments are now underway with laboratory cultures of *Morpho* to study the mechanism of feeding regulation. The difference with respect to microhabitats seen in the field suggest a photoperiodic response within 24-hour periods.

The variations in peak feeding periods seen for different instars of *Morpho peleides* (Fig. 3) is further evidence that feeding behavior is initiated by changes in light intensity. These variations may be accountable in terms of the resting positions of larvae, relative to their exposure to unobstructed sky. While the resting positions of third, fourth, and fifth-instar larvae are generally lower on individual host plants than resting positions of younger larvae, these older larvae are invariably exposed directly to the sky and this direct sunlight—an important observation in interpreting the shift in peak feeding periods of older

larvae. Thus while such larvae are generally concealed in shaded places, where they rest on branches (Fig. 4), they have unobstructed visual contact with the sky and the changes in light intensity occurring throughout the day. Younger larvae, on the other hand, being confined to resting positions on the undersides of leaves (Fig. 4), while physiologically capable of responding to the same light intensities of older larvae, do not register the same intensities of light as do older larvae, at the precise same time of day—there will be a displacement of their time of response which is proportional to the degree of shading they are experiencing under leaf cover. Assuming that larval activity is triggered by temporal changes in light intensity, first and second-instar larvae should begin to feed earlier in the afternoon than older larvae, and later in the morning than older larvae as seen in the data on feeding activity of different instars (Fig. 3).

It is unlikely that the mechanism for this feeding activity pattern involves rhythmic changes in sugar levels and other metabolites within host plant tissues since the level of desired nutrient substances such as sugars would be minimal during the dawn hours. Other environmental influences such as diurnal temperature and humidity changes, known to act as sensory cues in the feeding behavior of some lepidopterous species (Dethier and Schoonhoven, 1968), cannot be ruled out here, but it appears that diurnal change in light intensity is the major factor initiating dawn-dusk feeding.

**THE ADAPTIVE SIGNIFICANCE OF DAWN-DUSK FEEDING:** In light of the high species density associated with tropical wet forest habitats (e.g., MacArthur, 1969), it is interesting to consider the possible adaptive significance of "dawn-dusk" feeding behavior as a specialized defense strategy in larval *Morpho peleides*. With the exception of the fifth-instar, the larvae are gaudily-colored in a mosaic of bright yellow and red patches and lines. At the fifth-instar, larvae become a dark brown, lose the large yellow patches, and appear more cryptic than younger larvae. By the time larvae become late third instars, they are too large to stay on the undersides of *Machaerium* leaves during long resting periods, and conceal themselves on branches near the ground, in heavy shade, (Fig. 4). I interpret this behavior as a means of escape from birds and other small insectivorous vertebrates (lizards and frogs) which are active at different times of the day and night. Concealment of first and second instar larvae on the undersides of leaves functions in the same manner as resting on low branches in heavy shade. The question as to whether or not *Morpho peleides* is palatable to potential vertebrate predators is somewhat puzzling. I documented substantial adult mortality in this butterfly species, presumably the result of avian predation. Dr. Alexander F. Skutch since tells me that the Rufous-tailed Jacamar, *Galbula ruficauda*, captures many butterflies, including species of the genus *Morpho*, at various elevations of wet forest in Costa Rica. The bright coloration of the larvae suggests unpalatability, as indicated by lab-

oratory studies of other groups of unpalatable adult butterflies (Brower and Brower, 1964). Apparently such phytophagous insects receive their protection (unpalatability) from their own predators by storing within their bodies phenolic and other classes of secondary plant compounds (Von Euw, Reichstein, and Rothschild, 1969; Brower, Brower, and Corvino, 1967). Since feeding experiments using *Morpho* as prey for caged birds have not been performed, it cannot be said conclusively that larvae are unpalatable. Indirect evidence of unpalatability has been observed when larvae of *Morpho peleides* disturbed in the laboratory, produce a volatile substance that has a strong vinegar odor. This substance is secreted by a small orange gland situated between the first pair of true legs. During emission, the larva raises itself so that the gland becomes exposed; this is accompanied by a waving motion of the anterior end of the body, presumably as a means of aiming the gland in the direction of potential danger. The entire event lasts about 10 seconds. This behavior and the irritating sensations produced by the dorsal tufts of hairs have been observed in two subspecies of *Morpho peleides* (*limpida* in Costa Rica and *hyacinthus* in El Salvador) and at least one subspecies of *Morpho polyphemus* from El Salvador (Young and Muysshondt, 1972c).

Studies on papilionidae (Eisner 1970; Eisner et al., 1971) indicate that such properties of *Morpho* larvae may function as defense mechanisms rendering them undesirable as prey for vertebrate predators. Parasitism of larvae is common in natural populations (Young and Muysshondt, 1972a) and presumably such substances do not deter attack by hymenopterous or dipterous parasites. Attack by predatory insects, such as ants, has not been observed. *Morpho peleides* larvae may obtain defensive compounds directly from foliage (i.e., volatile turpines or other phenols) or else synthesize these compounds using precursors obtained from foliage. If larvae are unpalatable, then the striking bright coloration can be interpreted as aposematic, although direct evidence for this is lacking at the present.

Assuming that larvae are protected against their predators, the existence of high predation rates on adult *Morpho peleides* suggest palatability. If it is assumed further that adults retain the palatable properties of their larvae, a plausible explanation of such predation could reside either in the feeding behavior of the predators, or through automimetic complexes in which such predators encounter palatable individuals. For the first explanation, it is known that some species of tropical birds feed selectively on certain parts of the bodies of lepidopterous larvae and adults (i.e., some birds pull out the intact digestive tract by the head of unidentified larvae and apparently devour only the remaining body tissues) (Young, pers. obs.). However, there is no evidence of such selective feeding on *Morpho* larvae. A more reasonable explanation is concerned with the apparent broad local larval host plant specificity exhibited by *Morpho peleides* (Table 1) and the possible occurrence of local complexes of



automimicry within this butterfly. Automimicry has been previously studied for a single species of butterfly (the Monarch) in which it was found that this species occurred as several geographical varieties, exhibiting a broad spectrum of palatability (Brower, Brower, and Corvino, 1967; Brower, 1970). Brower, Pough, and Meck (1970) discuss the adaptive significance of automimicry for butterfly populations with respect to avian predation. Unlike the automimicry discovered in the Monarch Butterfly, *Danaus plexippus*, (Brower, Brower, and Corvino, 1967; Brower, 1970), in *Morpho peleides*, such an advantage is defined within local populations, rather than among different geographically separated populations. In terms of the model presented by Brower, Pough, and Meck (1970), their parameter  $m$  (the number of prey per predator) may be large for local populations of *Morpho peleides* since the distribution of this species may be less patchy than that of other species possessing a narrower host plant specificity. Localized increase in  $m$  should enhance the effects of automimicry as a mechanism for lowering predation rate. Assuming the existence of automimicry in *Morpho peleides*, the adaptive significance of dawn-dusk feeding in the aposematically-colored larvae of this butterfly becomes accountable.

The most plausible explanation for the evolution of distinct bimodal "dawn-dusk" feeding strategy in an aposematic species is that local larval populations consist of a series of palatable and unpalatable varieties in which frequencies of the varieties are so similar that would-be vertebrate predators encounter unpalatable and palatable individuals equally. In this hypothesis, the dawn-dusk feeding activity pattern ensures survivorship of both palatable and unpalatable larvae from predation by vertebrates. It is known that the cardiac glycoside content of various species of Asclepiad plants varies qualitatively and quantitatively and the palatability of Monarch butterflies whose larvae feed on them comprise a spectrum of palatability ranging from completely acceptable to completely unacceptable (Brower, 1970). It is also known that most plants have complex mixtures of phenols that vary among related species, and even among different populations of a single plant species (Levin, 1971). While the function of phenols actually isolated from the wings of certain butterflies (Ford, 1941; Morris and Thomson, 1963; 1964) is unknown, it is possible that some species obtain defensive properties, similar to those demonstrated for cardiac glycosides, alkaloids, and other secondary plant substances taken up by other insects (Brower, Brower, and Corvino, 1967; Von Euw, Reichstein, and Rothschild, 1969). It is plausible that the host plants of *Morpho peleides* (Table 1), while all members of the Leguminosae, represent different ensembles of secondary plant substances (probably phenols) that endow their herbivores with different degrees of palatability. Careful searching would probably reveal additional host plants of this butterfly, on a local basis, lending further support to this hypothesis of automimicry. Experimental feeding studies involving larvae placed on different host plant species must be done. In El Salvador, *Morpho polyphemus*

feeds on *Paullinia pinnata* (Sapindaceae), in addition to a variety of legumes, including *Inga* sp. and *Machaerium salvadorensis* (Young and Muysshondt, 1972b). Natives of El Salvador use crushed leaves of *Paullinia* as a fish poison ("Barbasco").

Substantial evidence of predation on adult *Morpho peleides* in Costa Rica was found in automimetic assemblages it is possible that a substantial portion of the adult butterflies would be acceptable as prey and therefore such a population could in fact experience extensive avian predation, depending to a large extent upon foraging habits of the birds (i.e., Jacamars) involved. Unlike larvae of *Morpho peleides* which can evolve a daily feeding strategy adjusted so that maximal activity occurs at times of the day when vertebrate (visual) predators would be least likely to detect them, adults of this species are least active when many insectivorous birds forage. Substantial predation on adults is predicted in localities where the species is common and exploits different larval host plants. An alternate explanation for high adult mortality would be that individuals become more acceptable as prey as they complete ontogeny. Perhaps only the first four larval instars are unpalatable, with the fifth instar becoming palatable and resulting in a palatable adult. It is known that the fifth instar larva of *Morpho peleides* is cryptic in appearance, unlike the earlier instars which are very gaudily-colored (Fig. 4; Young and Muysshondt, 1972a). Such a change in coloration may be associated with an increase in palatability during this instar since selection would favor the development of crypsis with increased acceptability as prey during ontogeny.

The local abundance of the unpalatable variety of *Morpho peleides* is a function of the relative numbers of unpalatable host plants in the area, the strategy of oviposition of female morphos, and the degree of adult population cohesiveness at breeding sites. Young (in prep.) found that adult populations of *Morpho peleides* at Cuesta Angel and Bajo la Hondura tend to be stable during periods of high recruitment and that females wander farther than males. Females presumably wander more than males as they search for suitable oviposition sites. This permits exploitation of many different kinds of host plants by the species.

DAWN-DUSK FEEDING AS AN ADAPTIVE STRATEGY IN MORPHO: Observations on the natural history of various Brazilian species of *Morpho* (L. S. Otero, pers. comms.) indicate that different species-groups exhibit marked differences in: host plant specificity at the family level, type of oviposition, and degree of larval gregariousness on host plants. However, unlike other groups of tropical butterflies (e.g., Alexander, 1961), distinct larval feeding patterns have not yet been studied in the genus *Morpho* and it is predicted that very different daily activity patterns of peak feeding exist in this group. From recent observations of both Brazilian and Central American *Morpho* (L. S. Otero, pers. comm.; Young and

Muyshondt, 1972a, b, c) several predictions on various adaptive ecological and behavioral traits for different species-groups of the genus *Morpho* have been summarized (Young and Muyshondt, 1972c). Of major interest here are contrasts in some of these traits predicted for Central American species of dazzling blue morphos" (*rhetenor*, *cypris* groups) and the "brownish morphos" (*achilles* group) discussed elsewhere in terms of adult behavior (Young, 1971b). Species of dazzling blue morphos are generally confined to the canopy of primary-growth lowland tropical wet forests, while species of brownish morphos (i.e., *Morpho peleides*) are highly distributed in both primary and second-growth wet forests along altitudinal gradients (Young and Muyshondt, 1972c). Dazzling blue morphos are specialized forest species in which local larval host plant specificity is narrow, females exhibit cluster oviposition, and larvae are usually gregarious. Brownish morphos are capable of exploiting second-growth plant communities, possess broad local larval host plant specificity (Table 1), single oviposition, and single (non-gregarious) larvae. Such ecological and behavioral traits of species in the *achilles* group are interpreted as being components of an adaptive strategy for successful colonization of less stable plant communities (early successional stages) in the wet tropics (Young and Muyshondt, 1972a, b, c).

The adaptive significance of dawn-dusk feeding in the larvae of *Morpho* can be predicted in terms of habitat selection by member species of the genus. It is hypothesized that only species with broad host plant specificity, encompassing a spectrum of palatability, will evolve such a feeding strategy. Thus, virtually all species in the *achilles* group should possess dawn-dusk feeding, since all of these species have broad local larval host plant specificities (Costa Lima, 1936; Seitz, 1924; Otero, 1971; L. S. Otero, pers. comm.). In species of *Morpho* having broad host plant specificity, and experiencing colonizing episodes into less stable tropical communities, such a behavioral trait, while possibly prolonging developmental time (egg-adult), serves to minimize encounters between larvae and their vertebrate predators depending upon vision as a means of locating prey. More specialized species-groups of *Morpho*, such as the dazzling blue and glossy white morphos typically associated with more stable tropical communities, are predicted to experience selection pressures disfavoring the development of dawn-dusk feeding in their larvae. While their larvae are also gaudily-colored, many of them not only possess narrow larval host plant specificities, but these host plants may be unpalatable. Being more specialized feeders, larvae of these species would not be dawn-dusk foragers since automimicry would be lacking in local populations. Therefore, larvae could complete development faster and thus stand less risk of attack by parasitic and predatory species of insects and other arthropods. The daily pattern of larval feeding in more specialized species of *Morpho* may therefore be erratic, completely diurnal, or perhaps completely nocturnal. All of these patterns have



been casually noted in various species of the genus (L. S. Otero, M. Barcant, pers. comms.). It is therefore predicted that species belonging to specialized groups such as the dazzling blue morphos, would experience lower predation rates, both as adults and larvae. Preliminary evidence supporting this view has been obtained for *Morpho amathonte*, a dazzling blue morpho, a species generally restricted to lowland wet forests. It is hypothesized that dawn-dusk feeding in the larvae of *Morpho peleides* and other members of the *achilles* group has evolved as an adaptive strategy in response to high predation rates from insectivorous vertebrates in second-growth plant communities, where oviposition is on a wide range of plant species. Predation rates from insectivorous vertebrates are predicted to be higher on potential prey species such as *Morpho peleides* in second-growth habitats since predators possess more generalized feeding preferences in less stable communities. Such a strategy would be less adaptive in species associated with more stable plant communities since they possess specialized host plant preferences and may be unacceptable as prey. Potential vertebrate predators in more stable communities would be more specialized feeders (e.g., Cain, 1969) and thus predation rates may consistently be lower on larvae irrespective of the palatability of the species. Clearly, experimental field and laboratory studies are needed to test these ideas.

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